

IS HIGH-FREQUENCY STIFFNESS A MEASURE FOR THE NUMBER OF ATTACHED CROSS-BRIDGES ?

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Abstract

Muscle stiffness is an important property for movement control. Stiffness is a measure for the resistance against mechanical disturbances in muscular-skeletal systems. In general muscle stiffness is assumed to depend on the number of attached cross-bridges. It is not possible to measure this number in vivo or vitro. In experiments, high frequency perturbations are used to obtain a measurement of stiffness. In this paper a simulation study is presented concerning the correlation between the number of attached cross-bridges and high-frequency stiffness. A model based on the sliding-filament theory was used for the simulation of dynamic contractions. It is concluded that these two methods of muscle stiffness determination do not yield compatible results during lengthening.

Introduction

Muscle stiffness is a measure for stability against possible perturbations during movement. Therefore, many efforts are made to determine the stiffness of muscle and fibers (e.g. [1], [2]). In experiments the so called high-frequency stiffness is measured, which is based on the assumption that the number of attached cross-bridges is not affected by small changes in length. The elasticity of the attached cross-bridges and series elastic structures determine the muscle stiffness. Because the cross-bridges act in parallel in a sarcomere, the number of attached cross-bridges is proportional to stiffness [3]. In this paper we focus on the relation between stiffness based on the number of attached cross-bridges compared to high-frequency stiffness. With a model based on the sliding-filament theory of Huxley [4] we determined stiffness in both ways under isometric and isokinetic conditions.

Methods

The model is based on the partial differential equation (PDE) of Huxley [4], which describes cross-bridge cycling during muscle contraction. This model was extended with a filament overlap function which defines the maximal number of available cross-bridges for attachment. Some further modifications were made to the original Huxley model to account for physiological structures in a sarcomere: a series elastic element (a linear spring) and a dashpot to account for the minor viscous effects, were incorporated.

The stiffness measurement based on the number of cross-bridges is just a simple count of the attached cross-bridges which are recorded in the cross-bridges distribution. The high frequency stiffness can be calculated from the force changes during a sinusoidal length perturbation of the sarcomere.

The contraction protocol was divided into three phases. The first phase is an isometric phase during which the tetanic force is developed. The second phase is characterized as the isokinetic phase, this phase is absent during the isometric contractions. During the final phase (e.g. post-stretch) the active isometric force is allowed to redevelop.

Results

The results of the isometric and concentric contractions are consistent with what can be expected. The high-frequency stiffness is proportional to the number of attached cross-bridges. During the simulation of the eccentric contraction we do not see this proportionality. The model does predict a force enhancement during lengthening. The enhancement is comparable to findings of Sugi and Tsuchiya [2]. But, during the lengthening phase a distinct decrease of the number of attached cross-bridges can be observed. During the active

post-stretch phase the number of attached cross-bridges recovers to a number equivalent to the new isometric level. When the same contraction protocol with length perturbations is used, a corresponding number of attached cross-bridges during the whole contraction can be observed. In contrast with this result, a considerable increase in the high-frequency stiffness is calculated during lengthening. During the active post-stretch phase the high-frequency stiffness reduces to an isometric level again.

Discussion

The simulations show a discrepancy between stiffness of a sarcomere and the predicted number of attached cross-bridges during lengthening. This is consistent with findings of Cholewicki and McGill [5]. Their simulations demonstrated that the number of attached cross-bridges decreased during isokinetic contractions. The high-frequency stiffness calculated with the model shows a remarkable resemblance with experimental data of Sugi and Tsuchiya [2].

Based on experimental data [2] and our findings it is very likely that high-frequency stiffness is proportional to muscle force. Moreover, the reduced number of attached cross-bridges during lengthening indicates an increase in exerted force per cross-bridge. Finally, it is concluded that high-frequency stiffness during lengthening is not compatible with stiffness based on the number of attached cross-bridges.

References

- [1] Julian, F.J. and M.R. Sollins (1975) "Variation of muscle stiffness with force at increasing speeds of shortening"; *J Gen Physiol*; 66; 287-302.
- [2] Sugi, H. and T. Tsuchiya (1988) "Muscle stiffness and force changes"; *J Physiol*; 407; 215-229.
- [3] Gordon, A.M., A.F. Huxley and F.J. Julian (1966) "The variation in isometric tension with sarcomere length in vertebrate muscle fibers"; *J Physiol*; 184; 170-192.
- [4] Huxley, A.F. (1957) "Muscle structure and theories of contraction"; *Prog Biophys Biophys Chem*; 7; 255-318.
- [5] Cholewicki, J. and S.M. McGill (1995) "Relationship between muscle force and stiffness in whole mammalian muscle: a simulation study"; *J Biomech Eng*; 117; 339-342.